On the Formation of Circular Muskeag in Tamarack Swamps.

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(PLATES 279–281.)

In 1892 observations made by the writer upon plant-distribution in the valley of the Minnesota led him to recognize and describe what were termed *tension-lines* between groups of plants established in their habitats. In addition to that principal tension between centrally and distally distributed floras arising from what was denoted as *equatorial pressure*, other tensions due to topographic conditions were defined as secondary and as minor tensions. "By the latter term there is not meant the forest and prairie delimitation, for that is to be referred in large part to the principal lateral tension, developed by equatorial pressure. The various topographical features of the Minnesota valley with its gorges, glens, vales, meadows, hills and headlands bring about slight but distinguishable segregations of floral elements. Between meadow and bluff there exists a minor tension-line; between swale and knoll on the prairie, between hill and ravine in the forest, there are to be discovered such minor tensions."* In this paragraph was laid the foundation for a series of studies in the zonal distribution of plants, and much interesting material has since been reviewed. In an extended paper not yet published, but read before the Botanical Society of America at the Buffalo meeting in 1896, and given in abstract in an American journal,† the zonal distribution of plants upon the *roches moutoneés* of a fresh-water archipelago and upon lake strand and sand-dune islands was discussed and certain intimate and remarkable connections between physiographic and plant-distributional conditions were indicated.

Zonal distribution was studied in 1893 by Ant. Magnin,‡ who described the *Carex*, *Phragmites*, *Scirpus*, water-lily, pond-weed and *Chara* formations which, by their sequence, mark the increasing depth of the water off shore in the lakes of the Jura. A month or two later *Equisetum* zonal distribution was noted in the

* MacMillan, Metaspermae of the Minnesota Valley, 596, 1892.

† The Botanical Gazette, 22: 218. 1896.

‡ Magnin, A. Recherch. Veg. Lac. du Jura. Rev. Gen. Bot. 5: 241. 1893.

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lakes of northern Minnesota* and in the following year numerous papers along this general line were published both in Amer ca and abroad. Pieters† adapted the formation classnication of Magnin to an American lake and the writer published a short account of two singular floating or anchored atolls of sphagnum which he had observed in central Minnesota.‡ The general facts are well brought together by Warming§ in his recent text-book, although with that too frequent disregard of American investigation which is a blemish to so much European compilation.

Such zonal limnetic formations occur in all parts of the world and afford fine examples of this type of distribution.

At present it is desired to call attention to the tension-line between sphagnum moor and the higher forest-clad ridges surrounding such moors as they exist in Minnesota. Sphagnum formations with the various attendant plants are commonly designated as *Muskeag* by the woodsmen of Minnesota, and the northern half of the State, in particular, furnishes many splendid examples of this type of plant association. The smaller muskeags are quite generally round or approximately elliptical in outline, while the larger ones, although preserving for the most part rounded outlines, are more irregular in shape. They occur abundantly in the neighborhood of the glacial lakes so characteristically disposed throughout the morainic region of Minnesota and are by no means confined to the belt of pines, for they may be observed about Minneapolis, in Chisago county and in the middle western counties of the State. Unlike the more ancient lakes of western Ontario and the international boundary region between Minnesota and Canada, these lakes have the typically rounded form of a glacial basin and rarely imitate in outline the long, rock-bound and irregular bodies of water so omnipresent in northern Canada.

The sphagnum moors or muskeags may be regarded as such glacial ponds or lakes in process of conversion to forest, and almost every imaginable transition may be found, from open lakes with

* MacMillan, C. Shore formation of *Equisetum limosum*. Bot. Gaz. 18: 316 1893.

†Pieters, A. J. The Plants of Lake St. Clair. Pamph. 1894.

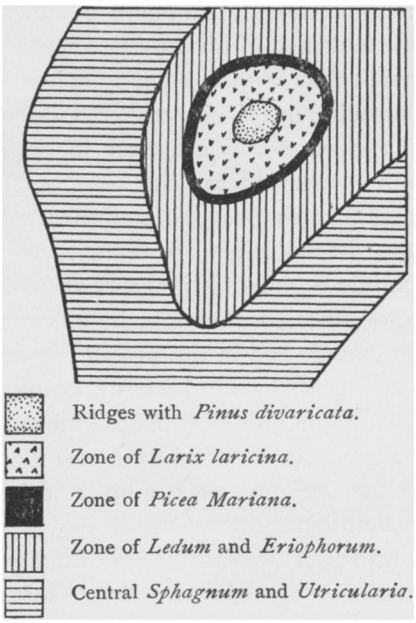
‡ MacMillan, C. On the Occurrence of Sphagnum Atolls in Central Minnesota. Minn. Botan. Studies, 1: 1. 1894.

§ Warming, E. Lehrbuch der Oekologishen Pflanzengeographie, 162. 1896.

sandy beach-lines continuous on all sides—a testimony to the untrammelled action of the waves—to solid masses of spruce and tamarack timber. The latter is displaced again by pines or hardwood and is converted eventually into mixed wood or perhaps even into meadow.

Typical muskeag with spruce and tamarack may clearly be taken as an intermediate physiognomic distribution of vegetation, linking the original open lake with the later glade or forest. A description of such an area may be given briefly and reference to the plates accompanying this paper will indicate clearly enough what relation the different plants bear to each other.

The center of the muskeag is ordinarily softer and more yielding than the edges, although this is not true of older specimens of



the formation. In them, and in many of the small muskeags, the center is quite as firmly filled with soil as the circumference. Towards the center of those younger muskeags, which will be considered as typical, there is a preponderance of the sphagnum. If the very center is occupied by an open pool, this is usually covered

with *Utricularia*, *Lemna trisulca*, or even pond-weeds and water-lilies. Farther from the center *Kalmia* and *Andromeda*, with such orchids as *Pogonia* and *Limodorum*, various species of *Carex* and *Eriophorum*, *Sarracenia*, *Salix*, *Vaccinium*, *Schollera* and kindred plants establish themselves. *Ledum* commonly affects drier and more peripheral positions, and is often the most abundant heath when the sphagnum has disappeared, except from isolated patches among the tamaracks. Surrounding this group of plants, herbaceous and shrubby, many of them with the pronounced xerophytic characters of sphagnum-moor inhabitants, are frequently spruces—either *Picea Canadensis* or *Picea Mariana*, but ordinarily the latter—tamaracks (*Larix laricina*) and sundry species of *Salix*, with *Alnus incana* and dwarf *Betulas*.

A very perfect series of muskeags, uninjured by fire or lumbering operations, occurs in the vicinity of Grand Rapids, Minn. I have been able through tne kindness of Mr. W. W. Pendergast, Director of the State Experimental Sub-Station at that point, to secure photographs of two of these moors, taken in such a way as to bring out the zonal distribution of the tamaracks and spruces. The general ridge group of plants in this region may be described briefly as forests of *Pinus divaricata*—the "Jack Pine" of the loggers. It is this tree which occupies the ridge in the background of Plate 279, to the left. Here and there in the valleys the muskeags are situated, each surrounded and, as it were, marked off from the pines by a circle of tamaracks. In the particular muskeag from which Plate 279 was taken the open area is almost elliptical in shape and contains about 1250 square rods. The ring of tamarack varies in width, but is estimated as about 75 yards across at the point shown. Where it faces the moor it is lined with black spruce. Small spruce trees are scattered out into the moor and a *Salix* shrub is seen in the foreground. The spruces nearest the open part of the moor are both smaller and younger than those farther back, although it must be observed that the difference in age is somewhat less than is indicated by the difference in size. Those growing out in the colder water and lighter peat soil are dwarfed in consequence. In this muskeag the principal accessory plants are *Andromeda*, *Chamaedaphne*, *Kalmia* and *Ledum*.

The following measurements and determinations of the age of trees in the muskeag and in its border-line were secured for me by Director Pendergast.

Tree.	Distance in rods in from border-line.	Diameter, inches.	Height, feet.	Age, years.
Spruce	0	5.5	28	49
Spruce	3	1.25	5	15
Spruce	6	4	17	38
Spruce	6	2	8	21
Spruce	6	2	8	21
Tamarack	0	7	30	55
Tamarack	2	2.5	12	45
Tamarack	10	1.25	6	18

Mr. H. B. Ayres, who has studied the habit of spruces growing in muskeag,* but publishes no comparative measurements, assures Director Pendergast that in cold bogs he has found black spruce little more than an inch in diameter and seventy-five years of age. A consideration of the table above will indicate, however, that the older trees are in general banked near the edge of the moor, while the trees that have pushed out into the moor, though much older than they appear, are actually younger than the individuals of the border-line.

The muskeag shown in Plates 280 and 281 is upon the Experiment Station grounds at Grand Rapids. The view shown in Plate 280 was obtained with the camera placed nearly under the trees of the opposite side and looking towards the northwest. Plate 281, taken from the same position, looks slightly southwest, and the two together give a very intelligent idea of the actual size and shape of the moor. In Plate 280, especially, the sharp demarcation between the zone of spruces facing the moor, and the zone of tamarack just behind is well brought out. *Eriophorum*, which did not appear in Plate 279 (the white flowers here being probably *Limodorum*), is abundant in the other two views and with *Carex*, *Ledum* and *Vaccinium* forms the principal secondary vegegation, the sphagnum being regarded as the primary group. Plate 281 shows tamarack facing the moor to the left, and spruces, with tamarack behind, to the right.

* Ayres, H. B. The Muskeag Spruce. Gard. and For. 7: 504. 1894.

An examination of the three views of the moors suffices to convince anyone that in the same sense that zones of *Carex*, *Phragmites*, *Scirpus*, *Nymphaea*, *Potamogeton* and *Chara* are described as characteristic of the limnetic distribution in the lakes of the Jura or elsewhere, so also are zones of *Larix*, *Picea*, *Ledum*, *Andromeda* and *Utricularia*, characteristic of the filled lakes or moors of Minnesota. It is scarcely worth while to designate the zones as *Laricetum*, *Picetum*, etc., for an indefinite number of such names might be found necessary in different parts of the world.

Certain points that have been touched upon might rightfully claim a more extended discussion. The presence of the spruce between the tamarack and the moor is peculiarly interesting. Large numbers of these muskeags form no spruce ring at all. This is especially true of those towards the southern limits of the formation, as for example near Minneapolis, which is south of the black spruce belt in Minnesota. In such cases the tamarack trees themselves stand facing the moor, and the transition is through *Salix*, *Cornus*, *Ilex* and kindred shrubby plants. A number of views illustrating this type of tension-line between moor or meadow and tamarack swamp have been obtained and may be published later. Apparently the exact habitat offered outside the sphagnum and inside the larch zone is seized upon by spruces, and they establish themselves where the water is too cold or the soil too thin for the tamaracks to flourish.

Cedar swamps offer a number of ecologic conditions that can not be entered upon here. Combinations of cedar and spruce in the tension line surrounding muskeag are met with. Their study is deferred until later.

In the case of the spruce trees established in their zone peripheral to the *Ledum* formation, the gradations in size connected as they are, under the reservations made above, with gradations in age, indicate that the tamarack and spruce rings are slowly closing in upon the central formations and should eventually occupy the whole area of the moor to the exclusion of those plants which flourish in the open. As a matter of fact, such circular or elliptical tamarack formations, solid clear to the core, are frequent in southern Minnesota, while in northern Minnesota a slight variation arises from the ordinary presence of a small central group of

spruces in such formations. Such tamarack swamps with central spruces are well developed in Cass county, Minnesota, especially in the vicinity of Gull lake, where I have studied them.

In any given instance it is apparent that several considerations should enter into a judgment concerning the probable origin of a solid or spruce-centered formation of tamarack. If the formation be a small one it may properly be questioned whether a stage with central moor had ever intervened. Furthermore, the contour of the bottom and depths of water in the original pond or lake would always have to be regarded in any generalization. For example, I have convinced myself that in some cases successions of muskeag openings with intervening tamarack arise from the filling of a lake with bars or reefs upon the bottom, the original positions of which is perpetuated by the lines of larches. Had the slant in the lake been strongly off-shore and the pond been deep in the middle a moor might then have been established at first with open water in the center, and only after a long lapse of years could the trees have crept out upon the peat. Had, on the other hand, the slant been slight and the pool sufficiently shallow at the center it might probably have filled without passing through any moor stage. Therefore some, at least, of the circular tamarack swamps with or without spruce cores could scarcely be regarded as necessarily derived from moors with tamarack or tamarack and spruce border-rings. This would, on the other hand, not hold true of all, and a consideration of the size and age of the trees from circumference to center will indicate that many of the solid tamarack swamps must have developed by this process of closing in a ring of timber upon a constantly diminishing moor.

Exceedingly pretty examples of the dispersion and obliteration of plants by such movements of tension-lines as here described may be observed. After the tamarack formation has become solid the sphagnum often manages to persist in little clumps and mats at the bases of trees where considerable rain water is drained into a small area by the tree trunk with its radiating branch system above. *Sarracenias*, *Vaccinums*, *Empeliums*, the dwarf cornel and other moor plants continue thus among the trees. The *Eriophorums*, *Salices* and many others do not seem to find the shade so grateful and commonly disappear altogether from the formation.

It will be noted that various generalizations upon the zonal distribution of plants might be based upon such facts as have been given above. Indeed it would seem that there are two principal types of plant arrangement in their habitats. These are: (1) Zonal and (2) Azonal. The first is connected either with environmental conditions as a principal factor, as in the case of the zonal distribution upon dome-shaped islands, upon *roches moutonées*, and on a larger scale upon mountain peaks and isolated ranges, along lake or ocean strand, and surrounding moors, or it may depend more particularly upon the character and habits of life of the plants themselves, as, for instance, in the care of the "fairy-ring" fungus. The matter may be summed up in a sentence. *Generally when there is well-marked radial symmetry in the topographic feature upon which a group of plants is distributed zonal arrangement is the response of the plant population to these symmetrical physiognomic conditions; but when the topographic feature is devoid of such well-marked radial symmetry the plants dispose themselves according to the azonal type.* Talus-heaps, flat extended meadows, highly irregular hills, shallow marshy ponds and other such localities may serve as illustrations of asymmetrical habitats. A variety of conditions determine whether the distribution upon a given area be zonal or azonal. And it is worthy of note that the same formation may in one case arise by zonal, in another by azonal distribution. This was brought out in the discussion of circular solid tamarack formations upon a previous page.

The contemplation of vegetation in any region with these principles in view is certainly illuminating. Practically it connects at once ecologic distribution with physiography, and enlarges the content both of topography and of botany.

Description of Plates.

Plate 279. Muskeag near Grand Rapids, Minn., showing the pine-covered ridge in background, and zones of tamarack, black spruce and *Ledum* in the foreground.

Plate 280. Muskeag near Grand Rapids, Minn., showing spruce zone against the tamarack, and a central moor with *Eriophorum*. Looking northwest.

Plate 281. Same muskeag as in Plate 280. On the left tamarack faces the moor; on the left the black spruce formation intervenes. The vegetation in the foreground is *Andromeda*, *Eriophorum*, *Carex* and sphagnum.

Plates all from photographs obtained for the author by Director W. W. Pendergast, of the Grand Rapids Experimental Sub-station, 1896.